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The white mangrove *Avicennia marina* in the Leschenault Inlet area

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Abstract

The white mangrove *Avicennia marina* (Forsk) Vierh forms local stands along the shores of Leschenault Inlet in three settings located in two main salinity regimes: the upper estuary where salinities vary from brackish water to hypersaline, and in the mainly marine Preston River Delta complex. At smaller scales, in the upper estuary *Avicennia* inhabits high tidal platforms, or front a steep dune shore where there is fresh water seepage. *Avicennia* is most common, however, in the Preston River Delta where there is daily marine tidal exchange. The three locations illustrate three different relationships between the occurrence and vegetation structure of *Avicennia* with respect to geomorphology and salinity. Within a given habitat, *Avicennia* occurs as scrub, heath, shrubland, and open shrubland and open heathland. Physiognomically, it forms single columnar-trunked shrubs, < 1 m high, varying to 3-4 m high, or multi-stemmed radially-branched shrubs 2-4 m high. Population structures of *Avicennia* cumulatively for the whole estuary show physionomic polymodality, and in various locations within its three main habitats there are adult-dominated populations different from seedling/sapling dominated populations. There have been changes in mangrove distribution and density over 60 years. The main changes are an increase of mangroves in the Preston River Delta, an increase in the extent of mangrove in front of the steep dune shore, and the establishment of small shrubs/saplings on high tidal platforms. *Avicennia* in Leschenault Inlet is scientifically important in that it represents the most southerly occurrence of this mangrove species in Western Australia. Five hypotheses are presented to explain this occurrence, ranging from a once widespread coastal distribution and then contraction to Leschenault Inlet during the latter Holocene, to *Avicennia* being only a recent late Holocene arrival to Leschenault Inlet. Preliminary analyses of pollen, and regional considerations suggest that *Avicennia* was not present along the south-west coast nor in Leschenault Inlet earlier in the Holocene. Later in the Holocene as more arid climates in Western Australia shifted northwards from Shark Bay to Exmouth Gulf and the shallow North West Shelf, the Leeuwin Current intensified, and *Avicennia* was established at Leschenault Inlet by delivery of propagules from northern populations. Its arrival in Leschenault Inlet may be a relatively recent event.

Keywords: mangrove, Avicennia marina, Leschenault Inlet, estuary, south-western Australia.

Introduction

As part of the collected papers on the estuarine environment of Leschenault Inlet, this paper describes local assemblages of the white mangrove *Avicennia marina* (Forsk) Vierh which forms local stands along the shores there. Despite being common and widespread in tropical Western Australia, the occurrence of *Avicennia marina* in this region constitutes a special situation in that it represents not only the most southern occurrence of the species in Western Australia but a disparate population with the next population some 500 km to the north.

While *Avicennia marina* in the Leschenault Inlet area has been noted in previous studies, reports, and surveys, no published study systematically describes its habitats and features of the vegetation. The first mention in the scientific literature of *Avicennia* in the Leschenault Inlet area was by Diels (1906) who noted the species (identified as *Avicennia officinales*) as part of a regional floral description, and also noted that it represented the most southern occurrence of the mangrove in Western Australia. Thereafter, mangroves in the Leschenault Inlet area have been noted in a variety of scientific publications (Sauer 1965; Smith 1985; Saenger *et al.* 1977; Semeniuk *et al.* 1978; Bridgewater 1982, 1985; Duke 1990 a,b, 1991).

Mangroves in Western Australia more typically occur in tropical environments as exemplified by the Pilbara Coast or Kimberley Coast, where there are mesotidal to macrotidal environments creating a complex array of habitats that support a variety of species (Semeniuk 1993a, b, 1996). The Leschenault Inlet area contrasts with these tropical settings in that it is located in a microtidal estuarine setting in a Mediterranean climate, extending the range of settings in Western Australia within which the species occurs.

The objective of this paper is to describe *Avicennia marina* in the Leschenault Inlet. The emphasis of the paper is on the description of the habitat setting of the mangrove, the structure and physiognomy of the mangrove, an inventory of the associated flora, and a description of the changes to the mangroves over the past six decades.

Methods

A variety of techniques were used to document the mangroves of Leschenault Inlet: examination of aerial photographs, establishment of transects through selected mangrove stands to document their relationship to habitats, site-based vegetation description, and laboratory analyses of soils, groundwater and soilwater.

Aerial photographs taken between 1941 and 1996 were used to define local geomorphic setting, determine the range of mangrove habitats available, and map the mangrove distribution in time. Transects through the mangrove populations were established to describe stratigraphy, depth to groundwater, soil types, and vegetation (Fig 2A), following Semeniuk & Wurm (1987). Transects were surveyed with

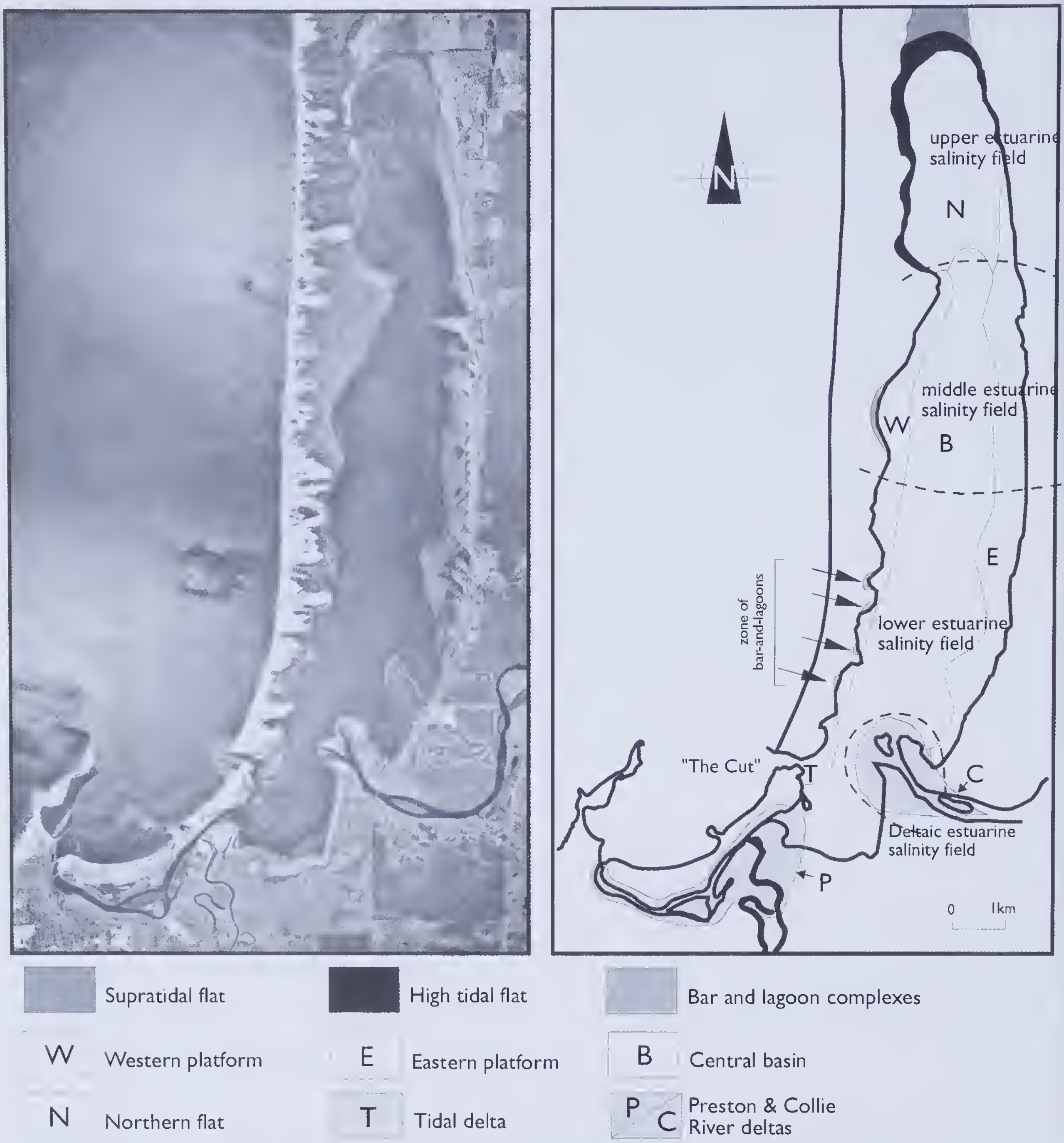


Figure 1. Aerial photograph (1966) of Leschenault Inlet showing nature of the elongate north-south oriented estuarine lagoon, and the deltaic complexes to the south prior to the anthropogenic impacts and map showing the distribution of estuarine units and salinity fields in Leschenault Inlet.

a dumpy level. Stratigraphy was determined by drilling and augering. Sediments in the stratigraphic sequence were described as to colour, fabric, texture and composition, and categorised to the main sediment groups of sand, muddy sand, sandy mud, and mud, and their shell-bearing equivalents. Piezometers were established at selected sites along transects to measure depth to water table and to sample water. Surface sediments for soil water determinations were collected at these selected sites, and frozen for transport and storage. Soil samples later were thawed and soil water salinity was determined following Semeniuk (1983). Salinity of groundwater samples and soil water samples were determined with a Cyberscan 200 TDS/Conductivity meter. Selected water samples were analysed for cationic content with an Atomic Absorption Spectrophotometer. Soil samples were wet sieved through standard Endecott Sieves at 1 ϕ intervals (Pettijohn 1957).

Vegetation structure, floristics, physiognomy, and the number of *Avicennia marina* individuals were documented and counted in replicate 5 m x 5 m quadrats along the

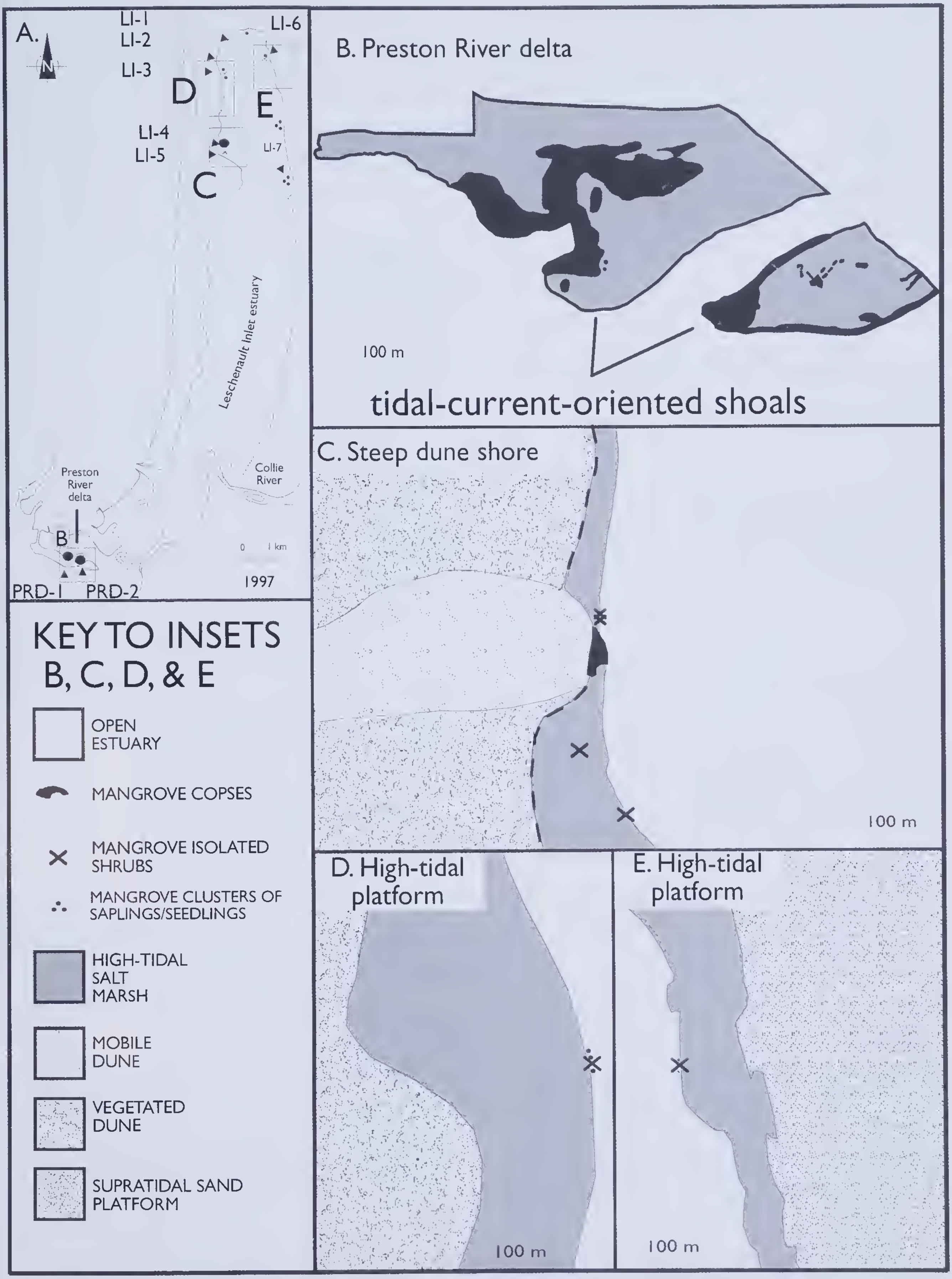


Figure 2. **A**: Location of study areas and transects. **B**: Map of mangrove occurrence in the Preston River delta, with mangroves mainly fringing the shoals. **C**: Map of occurrence of mangrove at the steep dune shore (advancing parabolic dune tip). **D & E**: Mangrove occurrence on the high tidal platforms.

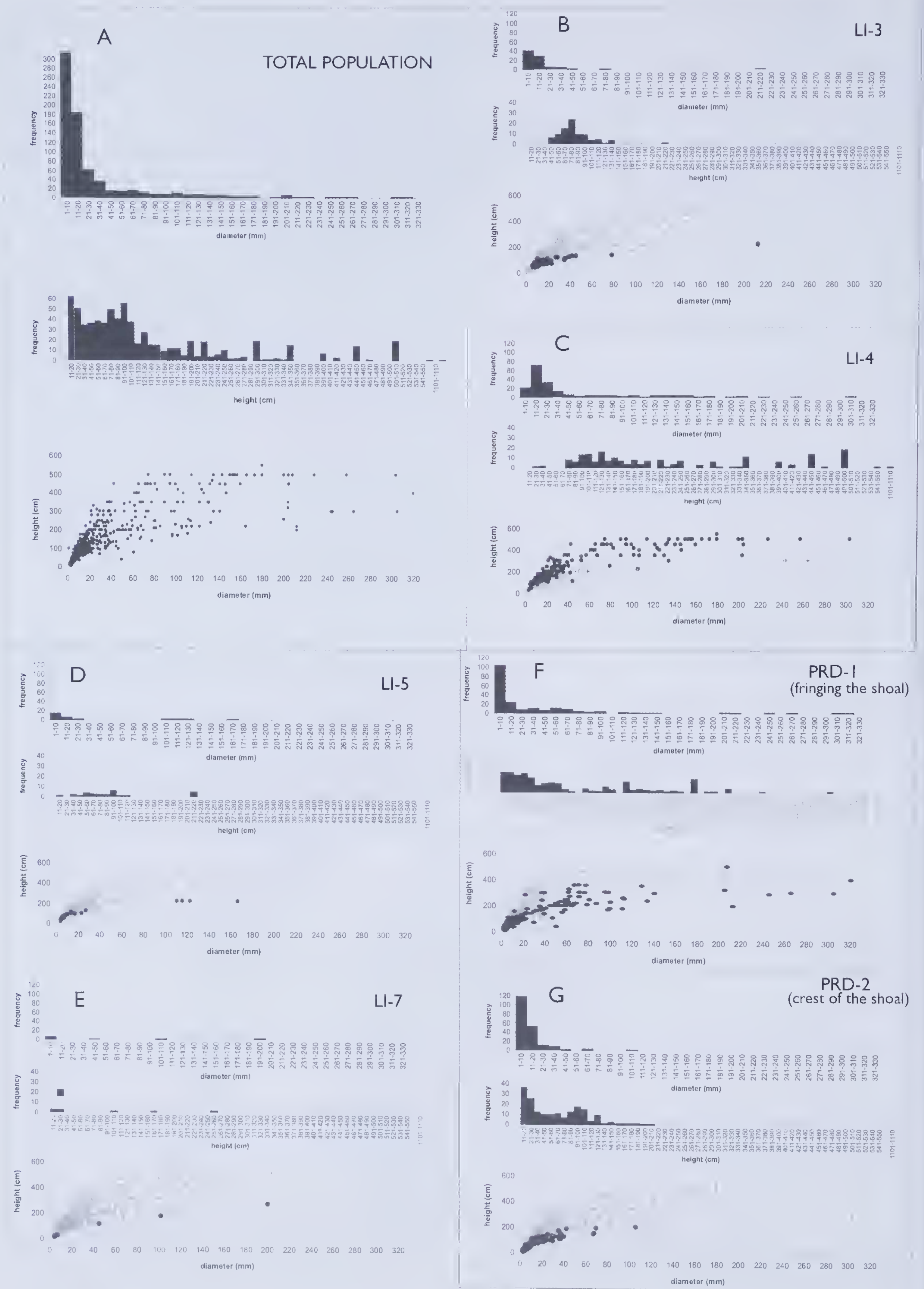


Figure 3. Population structures of *Avicennia marina*: legend continued over page.

Figure 3(continued): Graphs showing population structures of *Avicennia marina*. **A:** Total cumulative graphs for the whole of the Leschenault Inlet region. **B:** Graphs for Transect LI-3 (tidal flat platform). **C:** Graphs for Transect LI-4 (steep dune shore). **D:** Graphs for Transect LI-5 (high tidal platform). **E:** Graphs for Transect LI-7 (high tidal platform). **F:** Graphs for Transect PRD-1 (old stands fringing the tidal shoal crest of the Preston River delta). **G:** Graphs for Transect PRD-2 (recently recruited stands colonising the crest of a tidal shoal crest of the Preston River delta). While the data have been presented as plots for a given transect, specifically for the graphs of height *vs* diameter, the data for a given transect are presented against a background of the total cumulative graph of height *vs* diameter to illustrate seedling- or sapling-dominated patters, or adult-dominated patterns, or patterns of continuous recruitment against the total mangrove pattern.

Table 1. Terminology for and description of types of physiognomy of the mangrove plants at Leschenault Inlet estuary

Physiognomic term	Description of plant
seedling	generally single-stemmed plant up to 10 mm diameter and 30-40 cm high
sapling	generally single-stemmed plant up to 30 mm diameter, generally 30 or 40 cm high, up to 1 m high
young plant or shrub	single-stemmed plant up to 50 mm diameter, generally 1-2 m high
single columnar-trunked shrub	single-stemmed plant, generally 50-100 mm diameter, *ca* 1m high, varying to 3-4 m high
multi-stemmed erect- shrubs	generally 50-100 mm diameter, *ca* 1 m high, varying to 3-4 m high, locally 5 m high
multi-stemmed radially-branched shrubs	generally 50-100 mm diameter, *ca* 1 m high, varying to 3-4 m high, locally 5 m high
gnarled, recumbent, multi-stemmed radially-branched shrubs	generally 50-100 mm diameter, up to 300 mm diameter, 3-4 m high, up to 5 m high

transects. At a number of locations, representing the various habitat settings and physiognomic/structural types, *Avicennia marina* individuals were measured as to their height and trunk and stem diameter to describe the population in terms of size of mature plants, saplings and seedlings. Terminology for mangrove physiognomy is presented in Table 1 (and illustrated in Fig 7 of Semeniuk *et al.* 1978). Height was determined by a stadia marked in decimeters. Since measurement of stem and trunk diameters involved seedlings, saplings, young shrubs, and recumbent mature trees, measurement of DBH (diameter at breast height) was not possible. Trunk and stem diameters were measured at 10-20 cm from the ground. Measurements were obtained with a vernier calipers from two hundred plants from each selected locality.

Leschenault Inlet

Regional Setting

Leschenault Inlet is largely a shallow estuarine lagoon located along the coast within the southern part of the Swan Coastal Plain (Semeniuk & Meagher 1981), and in the Leschenault-Preston Sector of Searle & Semeniuk (1985). The estuarine lagoon is separated from the Indian Ocean by a barrier dune system, the Leschenault Peninsula (Semeniuk 1985a). The Leschenault Inlet estuarine lagoon is unique regionally in that it is the only estuarine system fronting the Rottnest Shelf that has been formed by a shore-parallel barrier dune complex, and that is wholly Holocene in age (Semeniuk 1985a).

Leschenault Inlet is set in a subtropical subhumid climate, or Mediterranean climate (Gentilli 1972), with an annual rainfall of 881 mm, an annual evaporation of 1984 mm. Tides are microtidal, usually diurnal, with a prevailing range of 0.5 m and a maximum range of 0.9 m.

From east to west, the three main landform and estuarine units bordering and constituting the Leschenault Inlet system are:

1. a high ridge of Pleistocene quartz sand and limestone, referred to the Mandurah-Eaton Ridge (Semeniuk 1997), and lowlands underlain by Pleistocene limestone referred to as the Yalgorup Plain (Semeniuk 1995a), both of which comprise the eastern hinterland;
2. Leschenault Inlet itself, which is an elongate shore parallel, shallow estuarine lagoon; and
3. a high quartz and carbonate sand dune barrier, the Leschenault Peninsula (Semeniuk & Meagher 1981), Holocene in age, that defines the western shore of the Leschenault Inlet.

The form of Leschenault Inlet, its internal features, and its shore types have been determined by several factors: the ancestral topography of the eastern hinterland (the Mandurah-Eaton Ridge and the Yalgorup Plain); the effects of a mid-Holocene higher sea level reworking the quartz sand of the Mandurah-Eaton Ridge; the orientation and extent of the Leschenault Peninsula; the eastward migration of parabolic dunes encroaching into the western margin of the estuarine lagoon from the Leschenault Peninsula barrier dune complex; and deltaic land buildups at the mouths of the Collie and Preston Rivers (Fig 1).

Prior to the 1950s, the Collie and the Preston River drained into the estuarine lagoonal environment. The Collie River formed a small wave-dominated delta (the Collie River Delta) to the south-east of the Leschenault Inlet, and the Preston River formed a tide-dominated delta (the Preston River Delta) in the southern part. The oceanic connection to the estuarine lagoon was via the river mouth of the Preston River (Semeniuk 2000).

A series of engineering activities from 1951 onwards has changed the nature of the estuarine lagoon and the river deltas:

- to facilitate exchange between the ocean and the estuary, a channel (known as "The Cut") was excavated through the southern part of the barrier dune opposite the Collie Delta, altering the hydrochemistry of the estuarine lagoon from one alternating from freshwater to saline to one dominated by marine conditions;

- much of the delta-land of the Preston River was infilled, thus severing the main body of the estuarine lagoon from the original oceanic exchange channel;
- the Preston River was diverted through a drain into the southern part of Leschenault Inlet; and
- the southern part of the Collie Delta was filled and drained for urban development.

Apart from local dredging for boat channels, and a rock-fill for a pipeline trestle, the nature of the internal geomorphology of the estuarine lagoon, however, has remained unchanged.

The central portion of the present Leschenault Inlet estuarine lagoon is a linear, shore-parallel, relatively deep mud-floored basin (generally 1.5-2 m deep). The eastern part of the lagoon where it adjoins the hinterland shore is a straight, shore-parallel, narrow, shallow water sand platform (tidal to about 1.0 m deep). The western part of the lagoon where it adjoins the barrier dune, has a multiple lobed shore as a result of the encroachment of parabolic dunes into the lagoon; the advancing front of the dunes has formed shallow water subtidal sand and muddy sand platforms and ramps (tidal to 1.5 m deep), and the inter-dune shores are protected small embayments underlain by mud and muddy sand.

Both east and west shores of the estuarine lagoon are mainly saltmarsh-vegetated high tidal platforms, the width varying from narrow (5-10 m) to wide (>500 m) depending on location in relation to mobile dunes, ancestral sand ridges, and erosional or depositional processes (Semeniuk 2000). The remnant of the Preston River Delta remaining after the construction of the harbour at Koombana Bay is a complex of linear, tidal-current-aligned shoals and emergent islands, with intervening shallow channels. The emergent islands are vegetated by samphires, rushes, or mangroves in the tidal zone, and terrestrial vegetation in supratidal parts.

There is a range of shore types developed along the periphery of the estuarine lagoon; these include (after Pen *et al.* 2000); 1) high tidal platforms vegetated dominantly by samphire or rushes; 2) tidal embayments (residing between dune corridors); 3) cliffed sandy shores where coastal erosion is incising into dunes; 4) steep dune shores where dunes are encroaching into the estuary; 5) bar and lagoon shores; 6) spits; 7) the Collie deltaic complex; and 8) the Preston deltaic complex.

There are three shore types that host mangroves (Fig 2): high tidal platforms; steep dune shores; and Preston River delta.

In terms of salinity structure, Wurm & Semeniuk (2000) subdivide the estuary into four zones, based on its variability over the seasons (Fig 1C): 1) an upper estuarine salinity field, where mean salinities approximate marine water, but show large variation in salinity, with brackish water common in the winter, and with hypersaline water in summer; 2) a middle estuarine salinity field, with mean salinities approximating marine water, but with moderate variation in salinity; 3) a lower estuarine salinity field, close to the marine source, where the salinities approximate marine water, with little variation; and 4) a deltaic zone, where the salinities approximate marine water, but exhibit marked freshwater patterns during flooding of the rivers.

There is a gradient of increasing groundwater salinity across the tidal flats, from marine at the water's edge to hypersaline towards the land. The hypersalinity is diluted by interaction with freshwater on a broad front from the barrier dunes, and is markedly diluted by freshwater seepage points from specific encroaching dunes (see below). The three main hydrologic sources and mechanisms pertinent to this study that maintain the mangroves are tidal recharge, freshwater seepage from dunes (Cresswell 2000), and meteoric recharge.

For tidal flat sites distant from freshwater seepage sites, the groundwater recharge mechanisms are tidal flooding and rainfall. During high tides and higher-than-normal prevailing winter water levels, estuarine water, largely of marine salinity, invades tidal flats and recharges the underlying groundwater. For sites proximal to barrier dunes, groundwater recharge is through tidal flooding, freshwater seepage, and rainfall. In regard to freshwater seepage, in winter, rainwater recharges groundwater under the dune barrier, and the water table rises forming locally steep hydraulic gradients along the shore (Cresswell 2000); these are the sites of freshwater seepage which reduce tidal flat salinities.

Avicennia marina in the Leschenault Inlet area

Some information on the biology and phenology of *Avicennia marina* in Leschenault Inlet area is in Semeniuk *et al.* (1978) and Duke (1990a, b, 1991). Duke (1991), using morphological characteristics and allozyme patterns, separated *Avicennia marina* into three groups (*viz A. marina* var *marina*, along the south-western and southern coast, *A. marina* var *australasica*, along the north-western to south-western coast, and *A. marina* var *eucalyptifolia*, along the northern and north-eastern coast). While Semeniuk *et al.* (1978) referred the species at Leschenault Inlet to *Avicennia marina* var *australasica* (Walp) Moldenke, later authors referred it to *Avicennia marina* var *marina* Moldenke (*cf* Tomlinson 1986; Duke 1991).

From a large scale habitat perspective, *Avicennia* occurs in Leschenault Inlet in two main salinity regimes: the upper estuary where salinities are variable from brackish water to hypersaline, and in the Preston River Delta complex. At smaller scales, in the upper estuary, mangroves inhabit high tidal platforms, or front a steep dune shore. The mangroves are best developed in the Preston River Delta setting, next in the steep dune shore setting, and least developed on high tidal platforms.

Within a given habitat, *Avicennia* occurs as scrub, heath, shrubland, and open shrubland and open heathland. Physiognomically, the mangrove forms single columnar-trunked shrubs, < 1m high, varying to 3-4 m high, or multi-stemmed radially-branched shrubs 2-4 m high. The population structures of *Avicennia* cumulatively for the whole of the Study Area, and in various locations within its three main habitats are shown in Fig 3.

To illustrate different aspects of population structure, data are presented in three ways: as stem diameters *vs* frequency, as plant height *vs* frequency, and as stem diameter *vs* plant height. The graph of diameter *vs* height illustrates, through occurrence of clusters of points and point outliers, the occurrence of recruitment phases in the populations. The graph of frequency of diameter classes next best illustrates population structure and recruitment phases.

The total cumulative data presented in Fig 3 illustrates the overall population structure of the Leschenault Inlet mangroves. The overall population structure for the whole of the study area shows a range of age classes, with a dominance of seedlings and saplings, grading to less abundant adults, reflecting the recent incursion of seedlings/saplings into the area. Population structures for the various populations in the three main habitats in the area are described below.

Apical extension and development of axillary shoots are a dominant form of canopy growth in the populations. There also is an abundance of lateral shoots (epicormic shoots) that develop and maintain branches in the adult plants. As the most southerly occurring outlier of *Avicennia marina* in Western Australia, phenologically there is variation in leaf growth and flowering and fruiting times compared to populations in tropical regions (Semeniuk *et al.* 1978). These observations are supported by the phenological studies of Duke (1990a) who compared phenology trends for Broome, Port Hedland, Carnarvon, and Bunbury as part of an Australia-wide survey. *Avicennia marina* in Leschenault Inlet generally commences flowering in March and April, with seed fall occurring in September (Semeniuk *et al.* 1978; Duke 1990a).

Avicennia in the Preston River delta complex

In the Preston River Delta area, *Avicennia* inhabits the tops and margins of tidally-aligned shoals and margins of emergent islands, respectively (Figs 4 & 5). These shoals and emergent islands are gently convex landforms, separated by shallow channels, and with upper surfaces located at *ca* mean sea level (MSL) to just above highest astronomical tide (HAT). Where bordered by narrow channels, the shoals or islands may be incised by the channel bank. Where bordered by broad channels, the edge of the shoal or island slopes moderately to subtidal. Landform, stratigraphy, substrate, groundwater and soil water salinity, and features of mangrove vegetation structure and density along Transect PRD-1 are presented in Fig 4. Salinity results of groundwater and soilwater in Transects PRD-1 and PRD-2 are presented in Table 2.

Stratigraphically, the shoals and islands consist of estuarine shelly sand capped by estuarine mud, sandy mud and muddy sand. Soils under the mangroves are bioturbated and root-structured muds and sandy muds. This mangrove setting is distant from any freshwater seepage, consequently salinity gradients vary from marine to hypersaline from estuary to the crest of a shoal, and locally reverses to brackish water in the centre of emergent islands where elevation is sufficient to allow rainfall recharge. Groundwater salinity under the mangroves varies from 19 000 to 36 000 ppm, and soil water salinity varies from 31 000 to 72 000 ppm (Fig 4; and Table 2).

Table 2. Salinity of ground waters, surface waters, and soil waters along the various transects. Sites are noted on the transects in Fig 4. Shaded rows are soil water results; other rows are water results.

Site	Date	Surface water (ppm)	Ground water (ppm)	Soil water (ppm)
LI 1A	25/03/98		52 000	30 464
LI 1AB	25/03/98		53 000	30 036
LI 1B	25/03/98		55 000	40 878
LI 1BC	25/03/98		39 800	30 840
LI 1C	25/03/98		2 720	7 533
LI 2 Inlet	25/03/98		38 300	
LI 2A	25/03/98		53 200	38 155
LI 2AB	25/03/98			163 654
LI 2B	25/03/98		52 400	79 156
LI 2BC	25/03/98			46 182
LI2C	25/03/98		3 290	6 799
LI 3 Inlet	25/03/98	32 100		
LI 3A	25/03/98		47 000	36 511
LI 3AB	25/03/98			33 824
LI 3B	25/03/98		64 100	33 362
LI 3BC	25/03/98			65 008
LI 3C	25/03/98		3 380	10 971
LI 4 Inlet	25/03/98	32 800		
LI 4A	24/05/97		40 000	32 959
LI 4A	25/03/98			29 225
LI 4A/1*	25/03/98		27 400	
LI 4A/2*	25/03/98		40 100	
LI 4B	24/05/97		35 800	32 780
LI 4B	25/03/98			33 908
LI 4B/1*	25/03/98		30 800	
LI 4B/2*	25/03/98		37 900	
LI 4C	24/05/97		26 600	
LI 4C	25/03/98			31 872
LI 4C/1*	25/03/98		2 150	
LI 4C/2*	25/03/98		3 770	
LI 4 D	24/5/97		1 020	
LI 4 D	25/03/98			39 467
LI 4D/1*	25/03/98		820	
LI 4 D/2*	25/03/98		667	
LI 5 Inlet	25/03/98	35 300		
LI 5A	24/05/97		36 400	37 980
LI 5AB	24/05/97	37 000	44 000	48 978
LI 5A	25/03/98		63 200	30 877
LI 5B	24/05/97	31 300		29 450
LI 5B	25/03/98		52 100	37 198
LI 5C	24/05/97		374	
LI 5C	25/03/98		25 500	29 905
LI 6A	25/03/98		20 000	31 094
LI 6B	25/03/98		6 760	11 063
PRD 1A	25/03/98		36 500	31 373
PRD 1B	25/03/98		39 600	37 983
PRD 1C	25/03/98		17 000	72 261
PRD 1D	25/03/98		19 400	19 258
PRD 2 Channel	25/03/98	25 100		
PRD 2A	25/03/98		27 500	15 047
PRD 2B	25/03/98		32 800	28 342
PRD 2C	25/03/98		32 300	31 290
PRD 2D	25/03/98	26 600		
PRD 2D	25/03/98		32 300	27 832

1* = before bailing; 2* = after bailing

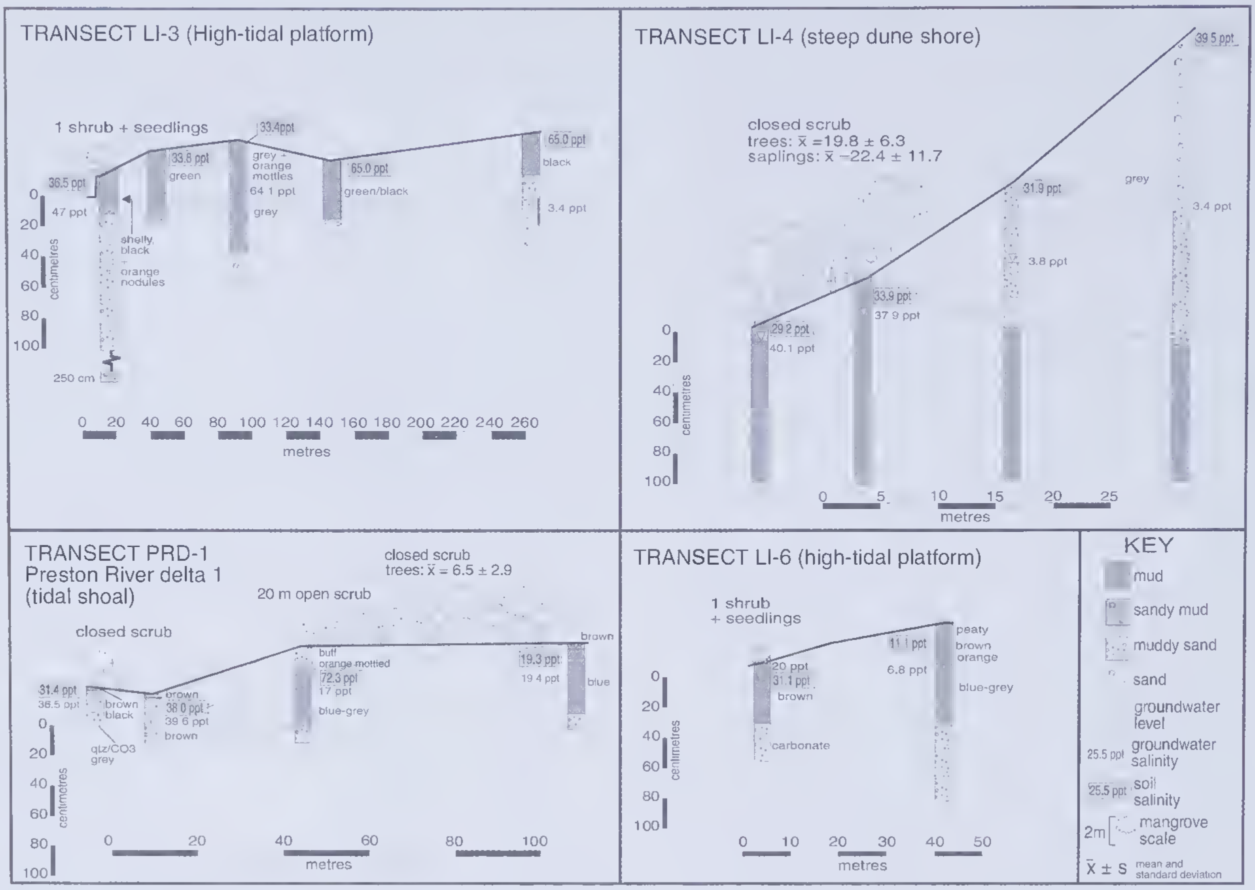


Figure 4. Profiles showing geomorphic and stratigraphic setting, groundwater and soil-water salinity, and information on the mangrove stands in terms of width of stand, height of stand, structure, and density.

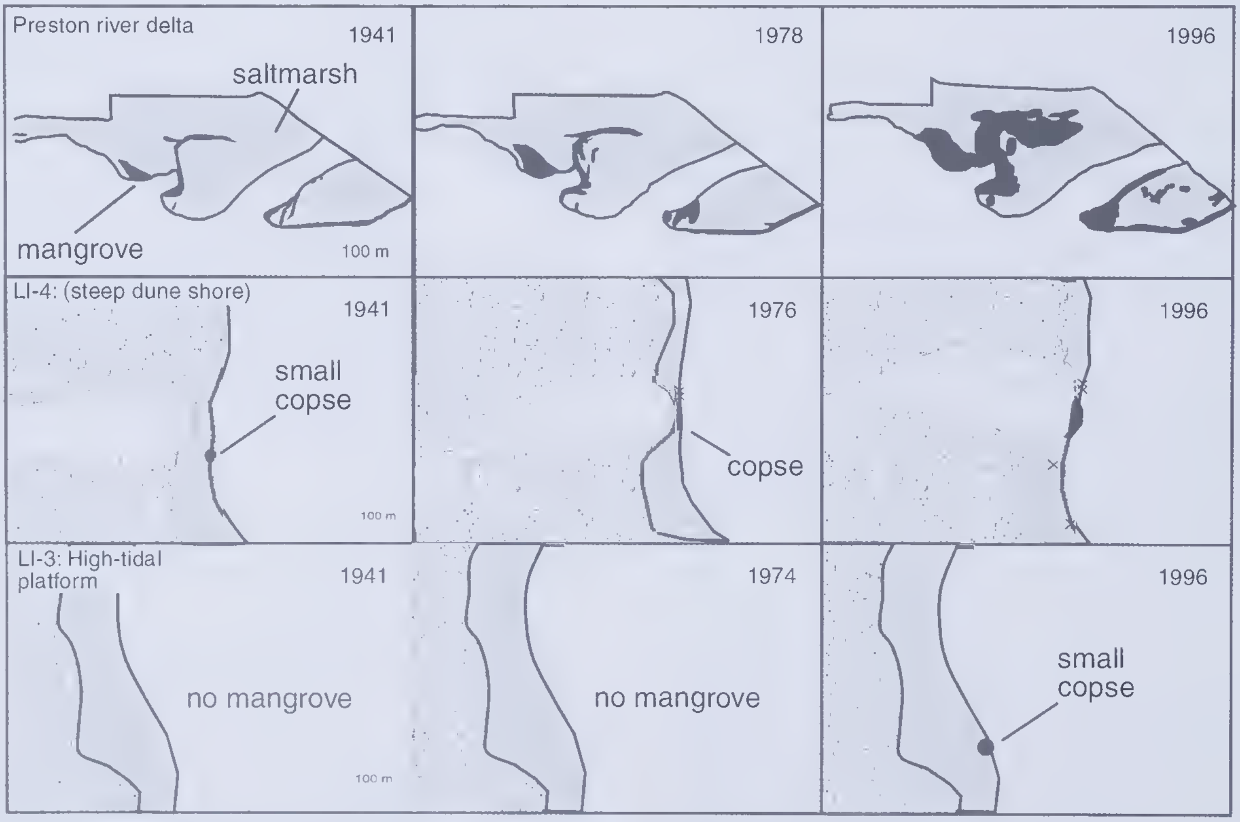


Figure 5. Changes in the extent of the mangrove in three habitat settings, *viz* the Preston River delta, the steep dune shore at Transect LI-4, and the tidal flat platform at Transect LI-3, based on aerial photography in 1941, 1974, 1976, 1978 (as indicated), and on ground-mapping and aerial photography in 1996.

Where inhabiting the margins of shoals or islands, *Avicennia* forms a narrow fringe several metres wide of multi-stemmed erect to recumbent-trunked scrub and single-stemmed erect to recumbent scrub, grading upslope to heath, with individuals mainly single-trunked, 4 m to < 1m high. If the margin of an island is erosionally cliffed, the tidal interval for mangrove may be removed, and terrestrial vegetation or riparian vegetation (*e.g. Casuarina obesa*) directly adjoins the deltaic channel. Where crests of shoals are at the appropriate tidal height, *Avicennia* forms scrub generally some 20 m wide, but up to 70 m wide. Where inhabiting the crests of shoals in association with a halophytic low heath of zoned *Sarcocornia quinqueflora* and *Halosarcia halocnemoides* subsp *halocnemoides, Avicennia* forms open heathland or isolated individuals, mainly single-trunked < 1 m to 2 m high, often lining small creeks. In the Preston River Delta area, there are two types of populations as described below.

In the past two decades, the populations of *Avicennia* have encroached over the tidal shoals and their margins of the delta complex through the dispersion of seedlings. The population structures of the mangrove of this area for three sites are shown in Fig 3. Along the margins of the shoals, where the mangrove populations have been extant since before the 1940s, the population now is comprised of seedlings, saplings, and mature adults, with a weak indication of phases of recruitment evident in the point outliers in the graph showing mangrove height *vs* diameter. Elsewhere along the margins of shoals, where the mangroves have encroached in the past two decades, the populations are dominated by seedlings, saplings, and some shrubs. On shoal crests, where there has been a widespread encroachment of mangrove in the past decade, the population is dominated by saplings and seedlings (Transect, Fig 3G). Thus in areas where the populations have been extant since at least the 1970s, adult plants dominate, but there is every gradation from seedlings to saplings to young plants and adults. In areas where the populations have encroached since the 1980s, seedlings and saplings dominate, and there is an absence of adults.

Avicennia adjoining steep dune shores

Avicennia inhabits a narrow tidal flat apron fringing a steep dune shore. The steep shore is the advancing front of a parabolic dune that is encroaching into the estuary. The tidal zone in front of the steep shore is a gently inclined surface, located between *ca* MSL and HAT, terminated along its estuary margin by a small cliff. A transect through this habitat showing stratigraphy, substrates, groundwater and soil-water salinity, and features of mangrove vegetation structure and density is presented in Transect LI-4 in Fig 4.

The stratigraphy under the dune and the tidal flat consists of estuarine mud, with a prism of dune sand that interfingers with and grades into the muddy sand and sandy mud of the tidal flat. Soils under the mangroves are bioturbated and root-structured muds and sandy muds. This mangrove habitat adjoins a site of freshwater seepage, consequently, the salinity gradients vary from marine to hypersaline from estuary to land, and then reverse to brackish water at the site of the seepage. Groundwater salinity under the mangroves across the tidal flat varies from 37 000-40 000 ppm, with 3 400-3 800 ppm in the area of freshwater seepage, and soil water salinity varies from 26 000-35 800 ppm (Fig 4 and Table 2).

The mangroves form scrub and heath, some 15-20 m wide. Individual plants are small, single-trunk erect, to multi-stemmed erect, to locally, multi-trunked recumbent shrubs 4 m to < 1m high. While adult plants are dominant, there is a gradation from seedlings to saplings to young plants and adults.

In the past two decades, the population of *Avicennia* at this site has expanded. The population structure of the mangrove of this area is shown in Transect LI-4, Fig 3C. The mangroves here have been extant since before the 1940s, and the population is comprised of individuals from seedlings and saplings to mature adults, with no clear division recruitment phases. Essentially there has been continuous recruitment in the area for the past several decades.

Avicennia on high tidal platforms

Avicennia inhabits high tidal platforms that fringe the eastern and western shores of the estuary. These habitats are gently inclined to subhorizontal surfaces between *ca* MSL and HAT, commonly terminated along their estuary margin by a small cliff 10-30 cm high and bordered by mid-tidal to low-tidal sand flats and muddy sand flats. The surface of platforms locally may have shallow pools < 30 cm deep, or may be traversed by straight to meandering natural drainage channels generally 30-50 cm deep, locally up to 75 cm deep. Landward parts of the high tidal platforms are vegetated by *Juncus kraussii*, and more estuary-ward parts of the platform are vegetated by zoned *Sarcocornia quinqueflora, Halosarcia halocnemoides* subsp *bidens* and *Halosarcia halocnemoides* subsp *halocnemoides*. Transects through this habitat showing stratigraphy, substrates, groundwater and soil water salinity, and features of mangrove vegetation structure and density are shown in Transects LI-3 and LI-6 in Fig 4.

The stratigraphy underlying the high tidal platforms consists of estuarine sand or muddy sand, capped by root structured mud and sandy mud. Soils under the mangroves are bioturbated and root-structured muds and sandy muds. Since these mangrove habitats are distant from the dune shores and distant from any sites of freshwater seepage, groundwater recharge is through tidal flooding and rainfall. Groundwater and soil water salinity across the high tidal platform vary from 47 000-64 000 ppm and to 3 400 ppm in the zone of contact of the tidal flat with the barrier dunes, with 47 000 ppm in the area of mangrove habitation; soil water salinity varies from 33 000-65 000 ppm (Fig 4; Table 2).

The mangroves on the high tidal platforms tend to be very scattered to isolated, small, single-stemmed erect shrubs < 1 m to 2 m high, forming very open heathland emergent above a herbland. The vegetation associated with the mangrove is *Halosarcia halocnemoides* subsp *halocnemoides*, and *Sarcocornia quinqueflora*. Larger mangrove plants periodically flower, and often there is a mat of seedlings directly under the canopy in the pneumatophores of these plants, showing successful recruitment by seedlings from the overshading parent plant.

Aerial photographs from 1941, and observations from 1976 to 1987, indicate that *Avicennia* was generally absent in the high-tidal platform habitat in the northern part of the estuary, with only one occurrence along Transect 6 (extant since at least 1941). The populations of *Avicennia* along the high tidal platforms, however, have expanded since 1987. The population structure of the mangrove of this area is shown in Transects LI-3, LI-5 and LI-7 in Fig 3, and show the population dominated by saplings and seedlings, reflecting the recent incursion of mangroves into this area, and hence the youthfulness of the population.

Changes of mangroves through time

The aerial photographic record over six decades, and intermittent observations over 23 years indicate that there have been changes in the mangrove distribution and density in time (Figs 5 & 6). The main changes are the increase in abundance of mangroves in the Preston River Delta area, an increase in the extent of the population in front of the steep dune shore (Fig 5), the establishment of small shrubs and saplings on the tidal platforms, and the spread of mangroves in the northern part of the inlet.

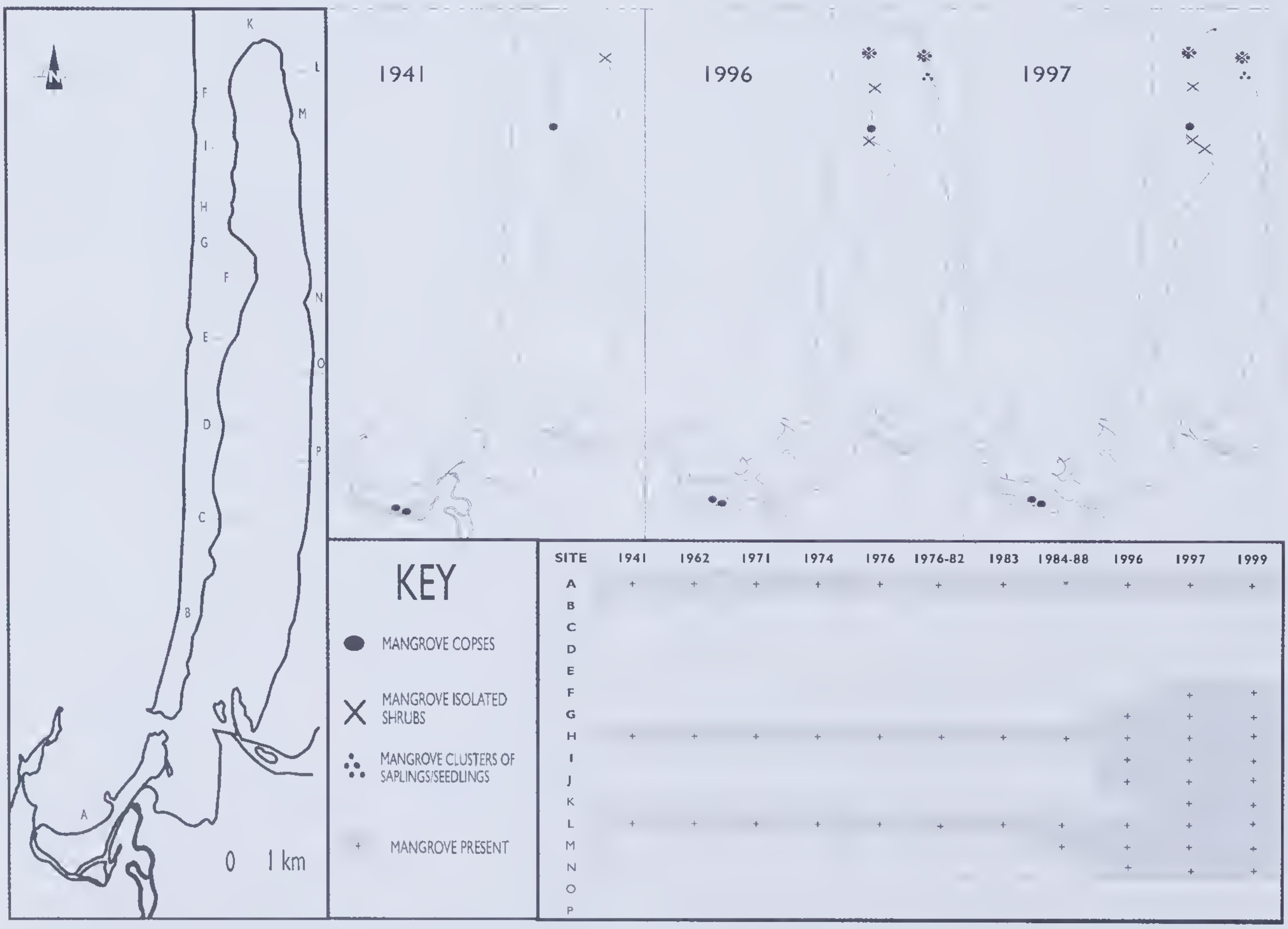
Discussion

Avicennia marina in Leschenault Inlet is discussed in terms of salinity fields as a major factor determining the occurrence and structure of the mangrove; the habitat approach, mangrove ecology, and anthropogenic impacts; the importance of freshwater seepage sites; the significance of the occurrences of *Avicennia* at Leschenault Inlet; hypotheses to explain the occurrence of *Avicennia* at Leschenault Inlet, evidence of the pollen record, and the biogeographic setting of the species.

Salinity fields and mangroves

The three settings of mangroves in the Leschenault Inlet area essentially illustrate three different relationships between the occurrence and vegetation structure of *Avicennia marina* with respect to salinity regimes:

1. Preston River Delta setting: a tidal flat with daily marine flooding; this is the normal and generally prevailing setting for *Avicennia* globally and elsewhere in Australia; as a result of the near-marine salinities, the mangrove forms well-developed scrub formations;



SITE	1941	1962	1971	1974	1976	1976-82	1983	1984-88	1996	1997	1999
A	+	+	+	+	+	+	+	*	+	+	+
B											
C											
D											
E											
F										+	+
G									+	+	+
H	+	+	+	+	+	+	+	+	+	+	+
I									+	+	+
J									+	+	+
K										+	+
L	+	+	+	+	+	+	+	+	+	+	+
M								+	+	+	+
N									+	+	+
O											
P											

Figure 6. Occurrence of the mangrove along various transects A-P, based on aerial photographic interpretation for the years 1941, 1962, and 1971, on aerial photographs and field observations for the years 1983 and 1996, and on field observations for the years 1976-1982, 1984-1988, 1997 and 1999.

2. steep dune shore setting: a hypersaline tidal flat with freshwater seepage to dilute the hypersalinity; this is a site of groundwater perturbation that allows mangroves to colonise saline environments (*cf* Semeniuk 1983); as a result of the near-marine salinities, again, the mangrove forms well-developed scrub formations; and
3. high tidal platform setting: a hypersaline tidal flat without freshwater seepage; as a result of the hypersalinity the mangrove occurs as scattered and isolated small individuals.

Habitats, ecology and anthropogenic impacts

This paper has documented the various formations of *Avicennia marina* within different habitat settings within Leschenault Inlet. It provides a baseline description of *Avicennia* in this region, and provides insight into the variety of edaphic, hydrologic, and hydrochemical environments that determine the occurrence of the species in an estuarine setting. In contrast to the richer variety of habitats that *Avicennia marina* colonises in tropical areas, Leschenault Inlet provides only a limited range, but nonetheless this can provide important information about mangrove ecology, in terms of the effects of stratigraphy, soils, tidal recharge *vs* freshwater seepage, hydrochemistry, hydroperiod, and nutrients, particularly since the species is at the geographic limit of its latitudinal occurrence in Western Australia. Where a species is at the limits of its natural geographic range, as *Avicennia* is in the Leschenault Inlet area, environmental determinants may be at threshold values for determining the species' response, and environmental effects thus may be amplified or exacerbated. For instance, the three habitat settings for *Avicennia* in the Leschenault Inlet area have different geomorphic, stratigraphic, hydroperiod, and hydrochemical features, and *Avicennia* has responded by developing populations with varied structural and physiognomic features. As such, these different habitat settings can function as valuable natural laboratories for research into the response of *Avicennia* to various physical, chemical and biological determinants of mangrove autecology.

For example, the anthropogenic alteration of Leschenault Inlet through harbour development and channel incision may have had a long-term effect on the mangrove populations. The slow expansion of *Avicennia* populations, and the slow general increase in height of the formations may be linked to the overall increased salinity of the estuary following the excavation of "The Cut", and the blocking through landfill of the Preston River Delta from its freshwater source so that now it is essentially a shoal-and island-clogged tidally flushed marine inlet. These engineering and hydrochemical changes, and the slow decadal-long response of *Avicennia* populations provide insight into determinants of *Avicennia* ecology in a regional context, but also underscore the problem that in situations where species are slow to respond to physico-chemical changes, that anthropogenic impacts may take decades to manifest.

Freshwater seepage sites

Maintenance of mangrove by daily tidal recharge is a well established process in tropical and temperate settings (Clarke & Hannon 1970; Chapman 1976; Tomlinson 1986), and the occurrence of mangroves in the Preston River Delta and on high tidal platforms conforms to this general pattern. Freshwater seepage also can be important in maintaining mangrove habitats, such as along upper tidal flats (particularly salt flats) in tropical environments (Semeniuk 1983). An important factor to emerge from this study is the association of mangroves with freshwater seepage, contrasting those maintained by tidal recharge (high tidal platforms and the Preston River Delta) from those partly maintained by freshwater seepage (steep dune shores). The importance of freshwater seepage thus is extended from tropical environments to Mediterranean climate settings.

The interaction between freshwater seepage and geomorphology to develop mangrove habitats in the Leschenault Inlet area, however, is subtle. While there is over 30 km of tidal flat circumferential to Leschenault Inlet, with development of wide high tidal platforms, there are only limited sites of freshwater seepage appropriately placed with potential to develop mangrove habitats. Along the western margin, for example, there is a general low level seepage of freshwater that results in kilometres of fringing *Juncus kraussii* rush between the dunes and the high tidal platform, the latter being colonised by herbaceous halophytes such as samphires. Also there are local more directed freshwater seepage sites manifest as perturbations in vegetation associations or as freshwater pools (Cresswell 2000). These general ubiquitous freshwater seepage interfaces and mosaics, however, are not inhabited by mangroves. Similarly, there are steep dune shores with freshwater seepage that abut the estuary margin, but the appropriate tidal level for potential mangrove growth is encompassed in a cliff.

Assessing the overall occurrence of fresh water seepage zones and mangroves in Leschenault Inlet leads to the conclusion that seepage zones, if they are to develop mangrove habitats, need to satisfy the following criteria:

- the freshwater seepage must be able to penetrate into the mid to upper tidal zone, where mangrove can colonise *i.e.* a steep hydraulic gradient in the freshwater system, or a distinct hydrologic pathway, or a linear incursion of a dune into the estuary that carries with it a finger of freshwater; and
- that there is no cliff along the estuary shore at the level where mangroves may be developed (usually, steep sandy shores are the most prone to wave attack, and hence develop cliff lines).

A summary of the various tidal environments in Leschenault Inlet, their relationship to freshwater seepage, and the reasons for the presence or absence of mangrove is presented below in Table 3.

In this context, it can be seen that the occurrence of *Avicennia* along the estuarine shore in zones of marked freshwater seepage is the result of distinct combination of geomorphic and hydrologic situations.

Significance of *Avicennia* at Leschenault Inlet

Avicennia marina in the Leschenault Inlet area, at latitude 33° 17' S, does not constitute the most southern occurrence of the species in the southern hemisphere globally. *Avicennia marina* occurs at higher latitudes in Victoria (Bridgewater 1982) at Corner Inlet (latitude 38° 45' S) and Western Port Bay (latitude 38° 22' S), and in South Australia, formerly as far south as Port Lincoln (latitude 34° 45' S), and is still extant as far south as Tumby Bay (latitude 34° 20' S). However, *Avicennia* in Leschenault Inlet is scientifically important in that it is the most southerly occurrence of this species in Western Australia, and as such it can provide valuable insights into climatic history and the dynamics of the Leeuwin Current. The nearest other coastal occurrence in Western Australia is along the coastal sector between Shark Bay and Carnarvon (latitude 24° 53' S), and the general nearest occurrence is offshore from the mainland at the Houtman Abrolhos Islands (latitude 28° 40' S). As will be discussed later, the mangrove stands at Leschenault Inlet, Houtman Abrolhos Islands, and Carnarvon may be inter-related.

Occurrence of *Avicennia* at Leschenault Inlet

Avicennia marina in the Leschenault Inlet area forms a very isolated occurrence in Western Australia. The nearest other locations of this species are the Houtman Abrolhos offshore from Geraldton, and Shark Bay on the mainland coast, essentially 500 km and 1 000 km distance, respectively. From a broader perspective, there are several critical regional maintenance factors that relate to the occurrence and survival of *Avicennia* in any given area (MacNae 1968; Walsh 1974; Chapman 1976; Oliver 1982; Tomlinson 1986; Hutchings & Saenger 1987): appropriate habitats, in terms of substrate, salinity, and low wave and tidal energy; adequate means of reproducing, either vegetatively or sexually; external seed source, if the population is not maintaining itself internally; adequately warm sea temperatures; adequately warm air temperatures; and no frost.

Table 3. Relationship between tidal environments, freshwater seepage and mangrove occurrence.

Setting	Description	Mangrove occurrence
dune abutting wide high tidal platform; freshwater seepage along the contact	Juncus kraussii developed along dune and high tidal flat interface	no mangroves - freshwater seepage developed above HAT
narrow, cliffed, high tidal platform; weak freshwater seepage from the upper slope	Juncus kraussii locally developed along HAT zone, no other vegetation developed	no mangroves - interval of potential mangrove occurrence encompassed in a cliff
steep dune margin cliffed at shore, with freshwater seepage from dune to estuary	sand cliff fronted by low tidal sand flat	no mangroves - interval of potential mangrove occurrence encompassed in a cliff
steep dune margin, with dune incursion into the estuary, and strong freshwater seepage into tidal zone	Avicennia marina developed in front of dune	mangrove present - appropriate tidal level developed, with freshwater seepage

Expression of these factors in the Leschenault Inlet area are listed in Table 4 below (data from Anon 1975; Pearce & Walker 1991; and this paper).

The other main estuaries along the coast between Shark Bay and Leschenault Inlet, termed here the Southwest-Coast Estuaries (including the estuaries of the Murchison, the Hill, the Moore, the Swan-Canning Rivers, and the Peel-Harvey system), though they have appropriate low energy tidal habitats and salinity, do not support *Avicennia marina* populations. These other estuaries, however, support halophytes such as *Haloscarcia* spp, *Suaeda australis*, and *Sarcocornia* assemblages (Cresswell & Bridgewater 1998) which colonise habitats (in terms of substrates, wave and tidal energy processes, and salinity) similar to mangrove habitats in Leschenault Inlet, and which cohabit with *Avicennia marina* in the Leschenault Inlet area. This implies that there are appropriate habitats for *Avicennia* in these other estuaries, yet there is a large gap along the coast with the mangrove absent between Leschenault Inlet and Shark Bay on the mainland, and the Houtman Abrolhos its nearest mangrove neighbour latitudinally. However, it should be

Table 4. Factors determining occurrence of Avicennia in Leschenault Inlet.

Maintenance factor	Expression in Leschenault Inlet
appropriate habitats	abundant in Leschenault Inlet
adequate means of reproducing	mangroves in Leschenault Inlet reproduce and maintain their populations both sexually and asexually
external seed source if population is not maintaining itself internally	potentially from northern waters via the Leeuwin Current
warm sea temperatures	derived from the Leeuwin Current
warm air temperatures	subtropical air temperatures; mean maximum summer temperature is 27.9 °C, mean minimum winter temperature is 8.3 °C
frost	frost is generally absent in the region of Leschenault Inlet

noted that other halophytic species are actually broadly distributed within the saline interior of the south-west region, and their origin today on south-coast estuaries could be related to the transport of seed by rivers. Such an avenue for distribution of plant species is not available to the mangrove.

We present and test five hypotheses to explain this distribution.

1. *Avicennia* was more widespread along the coast earlier in the Holocene with a more arid climate, but with a shift of aridity northwards over the late Holocene through Earth axis precession (Glassford 1980, Reichelt cited in Semeniuk 1995b), and the contraction of coastal populations to Shark Bay, mangroves at Leschenault Inlet are a relict outlier, surviving, but not linked to warm waters of the nearby Leeuwin Current.
2. *Avicennia* was more widespread along the coast earlier in the Holocene, as described above, but with a shift of more arid climates to the north over the late Holocene it remained at Leschenault, continuing to survive only because of the effects of the warm waters of the Leeuwin Current.
3. *Avicennia* was never present generally in estuaries, along the south-west coast earlier in the Holocene, and its occurrence at Leschenault Inlet initially was established by the delivery of propagules by the Leeuwin Current earlier in the Holocene when conditions were more arid; the population continues to be maintained by relatively warmer water where this Current impinges on the coast, in contrast to coastal areas immediately further north, and by the ongoing periodic delivery of propagules.
4. *Avicennia* was never present generally along the south-west coast earlier in the Holocene, and while the population at Leschenault Inlet initially was established by the delivery of propagules from the Leeuwin Current, the population continues to be maintained now by relatively warmer water where this Current impinges on the coast, and reproductively it is now internally self sustaining by adequate seedling production and survival without the need for periodic propagule delivery from the Leeuwin Current (this hypothesis is very similar to Hypothesis 3).
5. *Avicennia* was never present generally along the coast nor in Leschenault Inlet earlier in the Holocene, and as more arid climates in Western Australia shifted northwards from a centre on Shark Bay to Exmouth Gulf and the shallow North West Shelf (Semeniuk 1995b), the Leeuwin Current intensified, and the population at Leschenault Inlet was established by the delivery of propagules from northern populations late in the Holocene; as such, the arrival of the mangrove is a relatively recent event in the Holocene.

Hypothesis 1: *Avicennia marina* was once more widespread along the south-west coast, essentially occurring in all the southwest-coast estuaries between Shark Bay and Leschenault Inlet earlier in the Holocene, and since then, with a climate change, and a shift of the axis of aridity to further north in response to Earth-axis precession (Glassford 1980, Reichelt cited in Semeniuk 1995b), there was a concomitant shift and contraction of the species to the north. In this context, the occurrence of *Avicennia* at Leschenault Inlet would appear to represent a relict outlier population.

Evidence to partly support this hypothesis would be *Avicennia* pollen in Holocene sediment in other Southwest Estuaries. However, examination of appropriate Holocene sediments in the Swan-Canning River estuary, and the Peel-Harvey River estuary, the nearest neighbouring estuaries with similar tidal habitats, has not uncovered fossil *Avicennia* pollen. Absence of pollen as evidence for absence of the mangrove, however, is equivocal, because even if *Avicennia* was formerly present at these sites, long-term preservation of its pollen could depend on appropriate taphonomy and absence of bioturbation and reworking.

Another line of evidence for this hypothesis comes from archaeological studies in Shark Bay where Stevens (1994) concluded that it was possible that *Avicennia* populations were more widespread earlier in the Holocene, and that they had contracted in response to increasing basin water salinity (*cf* Hagan & Logan 1974), and in response to a possible Holocene climate change as the axis of aridity shifted northwards. From this perspective, the contraction of *Avicennia* populations in the Shark Bay area would represent a small scale pattern of a subcontinental-scale phenomenon *i.e.* the elimination of *Avicennia* from the Southwest Estuaries, and their contraction to the north. If this hypothesis is correct, then it would remain to explain why *Avicennia* remained as a relict population in the Leschenault Inlet area only.

Hypothesis 2: This hypothesis is similar to that above, but with an explanation as to why *Avicennia* was not eliminated from Leschenault Inlet as the zone of aridity migrated northwards, whereas it was eliminated from the estuaries further north. Such an explanation rests on the premise that coastal zones proximal to Leschenault Inlet today are bathed in warmer water than coastal waters located further north between Leschenault Inlet and Moore River estuary. Thus, with the shift of the arid climate to the north, and the elimination of *Avicennia* from the Southwest Estuaries, the species remained as a relict outlier of its once more extensive distribution because the Leeuwin Current provides a local warm water quasi-tropical setting in the Leschenault Inlet area enabling the species to persist.

Hypothesis 3: *Avicennia marina* occurs in Leschenault Inlet and solely in this region along the south-western Australian coast because eddies of the warm water Leeuwin Current periodically impinge on the coast in the Geographe Bay area, with some of this warm water deflected northwards as eddies towards the coast at Bunbury and into the Leschenault Inlet. Thus, there is potential that *Avicennia* propagules earlier in the Holocene, and up to the present, had been and are carried from northern more tropical waters. Once established in Leschenault Inlet, the relatively slightly warmer waters of the coastal zone maintained the populations. The dispersal of *Avicennia* propagules, traversing the 500 km between Houtman Abrolhos and Leschenault Inlet, may have involved direct delivery from the Houtman Abrolhos to Leschenault Inlet involving weeks of transport, or may have involved island-hopping.

A velocity of 0.2 m s^{-1}, at times 0.5 m s^{-1}, for the Leeuwin

Current, as reported by Cresswell (1991), could readily deliver *Avicennia* propagules from Houtman Abrolhos to Leschenault Inlet in 3-4 weeks. Clarke (1993) found that *Avicennia marina* var *australasica* propagules in south-eastern Australia can have medium term viability, surviving enforced dispersion for up to 5 months. A similar propagule viability for *Avicennia marina* var *marina* in Western Australia would implicate the Leeuwin Current as a possible direct delivery mechanism. Propagules from the region of Houtman Abrolhos would be entrained in the current and periodically delivered to the Bunbury area.

Alternatively, the *Avicennia marina* may have migrated from Houtman Abrolhos to Leschenault Inlet by island hopping *i.e.* there were small temporary sexually reproducing populations of *Avicennia* established on the string of islands and reefs located offshore from the mainland in the Cape Bouvard to Trigg Island Sector and the Lancelin to Dongara Sector of the Rottnest Shelf Coast (Searle & Semeniuk 1985), and these delivered propagules in turn along the chain of islands and reefs. This model would allow for dispersion of the species from island to island within the time of short term viability of its propagules. Currently, the islands and reefs offshore from the Western Australian mainland between Houtman Abrolhos and Garden Island do not support *Avicennia* stands, but given that these islands and reefs would have been larger earlier in the Holocene, and that with continuing bioerosion and wave erosion of these structures (Semeniuk 1985b), they have diminished to the size they are today, it is plausible that they lost their mangrove habitats over the period of the middle to late Holocene.

If Hypothesis 3 is correct, it would mean that *Avicennia* was not formerly more widespread along the mainland coast, and that *Avicennia* at Leschenault Inlet is not simply a relict residual population from these earlier times. The evidence to support this hypothesis includes the fact that the Leeuwin Current is a warm water, relatively fast moving offshore but shore-parallel current deriving from the tropical regions, that it carries tropical zooplankton and larvae, that it impinges on the coast in the vicinity of Leschenault Inlet, and that the other occurrence of *Avicennia* south of Shark Bay is in the Houtman Abrolhos Islands, in the path of the same current. From this perspective, the occurrence of *Avicennia* populations in the Leschenault Inlet area would represent a region where the Leeuwin Current interacts with the coast.

However, if Hypothesis 3 is correct, then it would remain to explain why *Avicennia* is absent from the Vasse and Wonnerup estuaries, where the Leeuwin Current *directly* impinges on the coast, and where marine seagrasses and algae in Geographe Bay reflect these quasi-tropical oceanic conditions. Its absence may be explained from a consideration of the original natural hydrochemistry of the Vasse and Wonnerup estuaries. Formerly, in the natural situation, both the Vasse and Wonnerup estuaries were largely barred and freshwater systems, and the fringing vegetation was/is *Melaleuca rhaphiophylla*, *Melaleuca cuticularis* and *Juncus kraussii*, indicating the extent of freshwater influence within the estuary. To place the significance of these species in hydrochemical perspective, in Leschenault Inlet, *Melaleuca rhaphiophylla*, *Melaleuca cuticularis* and *Juncus kraussii* along the tidal flat and dune margins indicate marked to very marked freshwater seepage to the extent that groundwaters approximate freshwater wetland systems. These freshwater-dominated habitats do not support *Avicennia* even though the species is present in the estuary. The species is best developed in the Preston River Delta complex (where there is daily exchange with marine water), and in the upper estuary where source waters became hypersaline and there is freshwater seepage to dilute this hypersalinity but insufficient to create a freshwater-dominated system.

Hypothesis 4: This is similar to Hypothesis 3, in that the Leeuwin Current earlier in the Holocene, perhaps under more arid conditions, originally delivered propagules of *Avicennia marina* to Leschenault Inlet, but once the mangrove population established, they became self-sustaining through vegetative reproduction and seedling production. Studies of population dynamics, fruiting, and seedlings over the past two decades show that mangrove populations within Leschenault Inlet indeed are self-sustaining and expanding through internal recruitment.

Hypothesis 5: This proposes that *Avicennia* is a very recent (late Holocene) arrival in Leschenault Inlet, reflecting a possible intensification of the Leeuwin Current as the maximum zone of aridity encroached onto the shallow waters of the Northwest Shelf. The Leeuwin Current then delivered mangrove propagules from northern populations.

Elimination of Hypotheses 1, 2, 3 and 4, and support of Hypothesis 5 rests on the fossil record of mangrove pollen in Leschenault Inlet and in estuaries further north, as described below (Semeniuk *et al.* 2000).

Evidence from the pollen record

The preliminary studies of pollen from the sedimentary record of Leschenault Inlet indicate that *Avicennia marina* was not present in the region earlier in the Holocene. The study of fossil tidal flat estuarine sediments from Peel-Harvey estuary and the Swan River estuary show that *Avicennia marina* may not have been present there earlier in the Holocene. The patterns of occurrence of *Avicennia marina* pollen in relation to stratigraphy and age are summarised in Table 5. More details for the pollen occurring within Leschenault Inlet, in terms of sampling sites and its taphonomy are provided in Semeniuk *et al.* (2000).

Milne (University of Western Australia, Department of Geography, *pers. comm.*) and Waterhouse (University of Western Australia, Department of Geology and Geophysics, *pers. comm.*) examined the palynological slides prepared from sediments described above, scanning 1 500 pollen grains for each slide to determine whether *Avicennia* was present. These data suggest *Avicennia* was not widespread along the south-western estuaries, and that it was not even present earlier in the Holocene in Leschenault Inlet. Effectively, Hypotheses 1-4 are eliminated. The limited data do, to date, support the suggestion that *Avicennia* is a very recent late Holocene arrival in Leschenault Inlet. If this is correct, and if it is linked to the shift northwards of more arid climates due to precession of the Earth's axis, this would suggest a possible intensification of the Leeuwin Current, or an intensification of warm water contribution from the Northwest Shelf into the Leeuwin Current, as the maximum zone of aridity encroached onto the shallow waters of the Northwest Shelf. The Leeuwin Current then delivered mangrove propagules from northern populations. The warm water impinging on the coast in the Geographe Bay to Bunbury area sustains the *Avicennia* population in the Bunbury area in quasi-tropical marine conditions.

However, these results must be viewed as preliminary, and it is suggested that a more wide-spread survey of estuarine tidal flat sediments in the south-western estuaries be undertaken to more conclusively determine that *Avicennia* pollen is absent.

Biogeography

Several authors have attempted to assign the mangrove populations of Leschenault Inlet to a biogeographic setting (Saenger *et al.* 1977; Semeniuk *et al.* 1978; Bridgewater 1985; Bridgewater & Cresswell 1999). In considering the species richness of mangrove assemblages along the Western Australian coast, Saenger *et al.* (1977) designated three mangrove regions, and placed the *Avicennia* populations of Leschenault Inlet into their southern region 5W Region, linking it with *Avicennia* in the Carnarvon/Gascoyne region.

Based on climatic considerations and species richness of mangrove assemblages of Western Australia, Semeniuk *et al.* (1978), delineated four mangrove biogeographic zones. The Gascoyne Delta, Carnarvon and Shark Bay region were linked with the Bunbury region, and placed in Biogeographic Region IV, all having only *Avicennia marina*.

Bridgewater (1985), in considering halophytic understorey in association with *Avicennia*, proposed that the *Avicennia* populations in the Gascoyne region represented the extremity of a cline from the Pilbara region, and that it would be better associated with the mangroves of the Pilbara, and isolated the mangroves at Leschenault Inlet as a separate region.

Bridgewater & Cresswell (1999) place the Leschenault

Table 5. Region-wide results of sampling for *Avicennia* pollen in Holocene deposits.

Setting for pollen sample	Age (years BP)	*Avicennia* pollen	Implications
sediment under modern mangrove scrub, Leschenault Inlet See Semeniuk *et al.* (2000)	modern	yes	mangrove pollen preserved, thus useful to infer occurrence of *Avicennia*
sediment in other estuarine environments in Leschenault Inlet See Semeniuk *et al.* (2000)	modern	yes	mangrove pollen preserved, thus indicating that Avicennia pollen is adequately dispersed to implicate its presence
recent fossil sediment, under saltmarsh flats along north, eastern and western coasts of Leschenault Inlet where there is no occurrence of mangrove today See Semeniuk *et al.* (2000)	< 1 000	no	mangroves were not widespread in the recent past in Leschenault Inlet
recent fossil sediment, under deltaic shoals of the Preston River delta, where there are mangrove nearby today See Semeniuk *et al.* (2000)	< 1 000	no	mangroves were not widespread in the recent past in Leschenault Inlet
fossil sediment at 2 sites under stranded tidal flats, Peel-Harvey estuary(Transect 3 of Semeniuk & Semeniuk [1991) and Transect 8 of Semeniuk & Semeniuk [1990]); no mangroves today	7 000-4 500	no	mangroves were absent from the Peel-Harvey Estuary, and thus were not more widespread along coast earlier in Holocene
fossil sediment under stranded tidal flats, Swan River Estuary (3 sites, in the upper to middle estuary *viz* Redcliffe Bridge, Garrat Road Bridge, and Ellam Street Jetty); no mangroves today	no date	no	mangroves were absent from the Swan River, and thus were not more widespread along coast earlier in Holocene
fossil sediment under river channel at 60 m below MSL (Churchill 1959); no mangroves today	12 000	no	though Churchill described the pollen-bearing sediment as a freshwater peat, the site was situated at depth along the valley tract of the Swan River, and potentially was the upland part of the Swan River estuary; if this is the case, it appears that mangroves were not present within Swan River estuary in the early Holocene

Inlet mangroves in a western transitional division named from the presence of the key species, *Avicennia marina* and *Halocarcia indica bidens* which extends from Leschenault Inlet to Shark Bay. If the hypothesis that *Avicennia marina* at Leschenault Inlet is linked to the mangroves of the Houtman Abrolhos Islands and Carnarvon/Gascoyne region via the Leeuwin Current is correct, then perhaps *Avicennia* at all these locations should be viewed as deriving from a single species pool, and should be regarded as a single biogeographic region. This accords with the classification presented in Bridgewater & Cresswell (1999). If, on the other hand, the hypothesis that *Avicennia marina* at Leschenault Inlet is truly a relict outlier, isolated from its tropical sympatriates for the latter part of the Holocene by a shifting climate, then perhaps the Leschenault Inlet and the Carnarvon/Gascoyne populations should be regarded now as separate biogeographic regions. Resolution of these questions must await further research, particularly into genetic comparisons of the populations. Bridgewater & Cresswell (1999) recognise 11 biogeographic divisions for mangrove and saltmarsh vegetation in Australia, and note that these compare well with regions derived from a broader set of attributes for the Interim Marine and Coastal Regionalisation for Australia.

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